Social communication in bats

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ABSTRACT

Bats represent one of the most diverse mammalian orders, not only in terms of species numbers, but also in their ecology and life histories. Many species are known to use ephemeral and/or unpredictable resources that require substantial investment to find and defend, and also engage in social interactions, thus requiring significant levels of social coordination. To accomplish these tasks, bats must be able to communicate; there is now substantial evidence that demonstrates the complexity of bat communication and the varied ways in which bats solve some of the problems associated with their unique life histories. However, while the study of communication in bats is rapidly growing, it still lags behind other taxa. Here we provide a comprehensive overview of communication in bats, from the reasons why they communicate to the diversity and application of different signal modalities. The most widespread form of communication is the transmission of a signaller’s characteristics, such as species identity, sex, individual identity, group membership, social status and body condition, and because many species of bats can rely little on vision due to their nocturnal lifestyles, it is assumed that sound and olfaction are particularly important signalling modes. For example, research suggests that secretions from specialized glands, often in combination with urine and saliva, are responsible for species recognition in several species. These olfactory signals may also convey information about sex and colony membership. Olfaction may be used in combination with sound, particularly in species that emit constant frequency (CF) echolocation calls, to recognize conspecifics from heterospecifics, yet their simple structure and high frequency do not allow much information of individual identity to be conveyed over long distances. By contrast, social calls may encode a larger number of cues of individual identity, and their lower frequencies increase their range of detection. Social calls are also known to deter predators, repel competitors from foraging patches, attract group mates to roost sites, coordinate foraging activities, and are used during courtship. In addition to sound, visual displays such as wing flapping or hovering may be used during courtship, and swarming around roost sites may serve as a visual cue of roost location. However, visual communication in bats still remains a poorly studied signal modality. Finally, the most common form of tactile communication known in bats is social grooming, which may be used to signal reproductive condition, but also to facilitate and strengthen cooperative interactions. Overall, this review demonstrates the rapid advances made in the study of bat social communication during recent years, and also identifies topics that require further study, particularly those that may allow us to understand adaptation to rapidly changing environmental conditions.

Key words: behaviour, Chiroptera, information, signals, sociality.

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I. INTRODUCTION

Communication is the process during which information is transmitted by a signaller and detected by a receiver (Bradbury & Vehrencamp, 2011). The signals transmitted convey important information to conspecifics, such as the location of suitable mates and dependent offspring, or alert individuals to the presence of predators and availability of resources (Balcombe, 1990; Blumstein & Armitage, 1997; Johansson & Jones, 2007; Chaverri, Gillam & Vonhof, 2010; Okabe et al., 2012). Other signals can carry information regarding position of group members, coordination of activities, invasion of territories by potential competitors or territory ownership, individual identity, and food unpalatability, among others (Snowdon & Boe, 2003; Scordato & Drea, 2007; Tibbetts & Dale, 2007; Kondo & Watanabe, 2009; Fichtel & Manser, 2010; Digweed, Rendall & Imbeau, 2012). The benefits to individuals involved in the process of communication are highly diverse, and while a few may be of relatively small relevance to fitness, a large number of signals transmitted during the process of communication can be essential to an individual’s survival and reproduction. Hence, understanding communication, from the reasons why animals communicate and what signals mean, to investment in signalling systems and optimal signal modalities, and even how humans modify an organism’s sensory environment, are all crucial to understanding evolutionary processes.

The topic of communication has permeated research in diverse areas, including computer science, psychology, linguistics, neurobiology, and animal behaviour. There are many seminal works that provide an extensive overview of animal signalling modalities and their evolution in different environments, of sensory systems and their costs, of sensory exploitation, and of the role of communication for diverse tasks that include predator avoidance, sexual selection, and social integration (Maynard Smith & Harper, 2003; Bradbury & Vehrencamp, 2011; Stevens, 2013). Many studies on communication have focused on ‘model’ species or taxonomic groups, such as bees, birds, primates, and other social mammals such as elephants and cetaceans. Unfortunately, research on animal communication in the two most diverse orders of mammals, rodents and bats, has lagged behind, yet the rapidly growing number of recent studies, particularly in bats, suggests that this is a potentially rewarding area of study.

Bats comprise the second largest order of mammals, with over 1300 species worldwide (Tsang et al., 2015). These mammals occupy most of the world’s ecosystems, and use an extraordinary diversity of feeding and roosting resources (Kunz & Fenton, 2003; Altringham, 2011). Some of such resources are highly ephemeral, and bats often feed on relatively unpredictable, but highly hurried, food items such as insect swarms or fruiting trees (Wilkinson, 1992; Dumont, 2003; Safi & Kerth, 2007). Although bats differ widely in their mating and social systems (McCracken & Wilkinson, 2000; Kerth, 2008), the majority of species are highly gregarious with colonies comprising up to several thousand individuals (Hristov et al., 2010; McFarlane et al., 2015). In addition to being gregarious, many bat species also form cohesive social units that remain together for up to several years (McCracken & Bradbury, 1981; Wilkinson, 1985; Chaverri, 2010), with important benefits to interacting individuals such as food sharing, communal defence, location of resources, cooperative care of young, and social grooming, among others (reviewed in Wilkinson et al., 2016).

The subject of social communication in bats has been previously partly reviewed elsewhere (Altringham & Fenton, 2003; Dechmann & Safi, 2005; Gillam & Fenton, 2016). These reviews focused primarily on sensory abilities, olfactory communication, and acoustic communication. Here we provide a comprehensive overview of communication in bats, from the reasons why they communicate to the diversity and application of different signal modalities exhibited by this large and diverse group of mammals. We end by suggesting potentially interesting and novel topics of research for future studies.

II. HOW DO BATS COMMUNICATE?

(1) Olfactory communication

Odour offers a way to emit signals that persist long after a signaller has departed. For this reason, it can be especially useful to convey persistent information in certain contexts, such as when bats use scent to mark territory limits (Buchler,
The importance of olfaction in nocturnal animals such as bats explains the large size of the olfactory bulb in their brains (Dechmann & Safi, 2005).

Volatile for communication are commonly secreted by specialized glands located on the body of many bat species (Scully, Fenton & Saleuddin, 2000; Dechmann & Safi, 2005), but they also may have a different origin. Many emballonurids, for example, use wing sacs which are cleaned and refilled daily with secretions from genitalia or the gular gland, saliva and urine (Voigt & Von Helversen, 1999). Hairs called osmetrichia, morphologically different from body hairs, are typically associated with glands and both hold secretions and are used by bats like paint brushes to apply odour to objects or conspecifics (reviewed in Altringham & Fenton, 2003).

Chemical variants of olfactory signals may be mixed in many unique combinations, thus offering a broad range of signals of individual attributes. By altering the number of compounds and their chemical composition, a remarkable diversity of odours is achievable, allowing bats to communicate different personal information (Brooke & Decker, 1996). Additionally, individual scent profiles may arise as a consequence of unique combinations of microbes in structures such as the wing sacs of emballonurids (Voigt et al., 2008).

(2) Acoustic communication

Acoustic communication is probably the most widely studied, and best known, signalling mode in bats (Dechmann & Safi, 2005; Gillam & Fenton, 2016). Sound is ideally suited for communication for many reasons. First, sounds can travel long distances and still retain the information necessary to convey messages (McComb & Semple, 2005; Reichard & Anderson, 2015), yet sounds can also be transmitted over very short distances with equal retention of critical information (Rowland et al., 2011). Acoustic signals are also known to convey a large diversity of messages, including individual and group identity, sex, age, size, aggression, social status, and hormonal condition, among others (Charlton, Zhihe & Snyder, 2009; Koren & Gfelen, 2009; Keen, Meliza & Rubenstein, 2013; Walter & Schnitzler, 2017). The messages encoded in acoustic signals can also be transmitted in a diversity of habitats, such as terrestrial and aquatic, and in a range of light conditions, including in complete darkness (Bradbury & Vehrencamp, 2011). In addition, sound is ideal for the process of pinpointing the location of specific individuals, as the location of the signaler can be determined with high precision (Naguib & Wiley, 2001). Compared to odour persistence, that of sound is ephemeral, but this is an advantage when the communication goal is to signal the exact time a given event occurs. Signal persistence may be achieved by broadcasting call sequences (e.g. Barlow & Jones, 1997).

Bats are known to use two types of sounds for communication, namely echolocation and social calls (Fenton, 2003; Dechmann & Safi, 2005; Gillam & Fenton, 2016; Russo et al., 2018, Fig. 1). Echolocation is primarily used for navigation and during the detection, classification, and localization of specific targets, particularly prey (Fenton, 1984; Schnitzler & Kalko, 2001). Echolocation call design has therefore primarily evolved to optimize echo generation (Barclay, 1999); yet these signals may also provide information regarding activities performed by vocalizing bats, such as acquisition of food, or specific information about individuals, such as sex or age, among others (Jones & Siemers, 2011; Gillam & Fenton, 2016; Finger, Bastian & Jacobs, 2017).

Although echolocation and social calls emitted by bats generally differ in structure due to specific functional adaptations (as reviewed by Bohn & Gillam, 2018), the evidence suggests the existence of a continuum between these types of signals (Fenton, 2013); the extreme flexibility in broadcasting echolocation calls makes them potentially suitable for conveying context-specific information (Fenton, 2003, 2013). Bats have been found to react to conspecific echolocation calls, suggesting that calls may convey information and elicit responses, and social calls may also include echolocation-like pulses, as in T. brasiliensis (Bohn & Gillam, 2018). For example, Noctilio leporinus flying in a group alter their echolocation call frequency to communicate their position more efficiently to conspecifics and thus decrease the risk of collisions in flight (Suthers, 1967); similarly, both Lasius borealis and Rhinolophus ferrumequinum seem to use cues from echolocation calls of conspecifics and modify their behaviour accordingly (Griffin, 1958; Mohres, 1967).

Echolocation calls are usually shorter than social calls, and are typically of higher frequency (Fenton, 2003; Pfalzer & Kusch, 2003; Ma et al., 2006). Thus, the main drawback of using echolocation calls to communicate is that high-frequency signals attenuate quickly (Griffin, 1971; Lawrence & Simmons, 1982; Hartley, 1989; Stilz & Schnitzler, 2012). For example, a bat with a hearing threshold of 20 dB sound pressure level (SPL) can detect a 20 kHz pulse emitted by other bats at 128 m; this range decreases considerably for pulses of 50 and 100 kHz, as these will be detected at a range of 35 and 16 m, respectively (Jones & Siemers, 2011). Considering that many species of bats emit calls above 50 kHz (e.g. Obrist, Boesch & Fleckiger, 2004; Jacobs, Barclay & Walker, 2007; Jung, Kalko & Von Helversen, 2007), the use of echolocation for communication in these species would be restricted to short-range interactions.

While social calls are often made of sequences of syllables (see Fig. 1), echolocation calls have relatively simple forms, which limits the amount of information the latter may encode (Beecher, 1989; Finger et al., 2017; Bohn & Gillam, 2018). However, using echolocation for communicating individual information can be better than using other signalling modes, acoustic or otherwise, as there is hardly any investment of energy in producing these vocalizations during flight (Speakman & Racey, 1991; Voigt & Lewanzik, 2012). Notwithstanding, the energetic investment required to produce echolocation pulses is significantly higher while resting (Dechmann et al., 2013). Another advantage of using
Fig. 1. Spectrograms of echolocation and social calls emitted by three Neotropical bat species, *Saccopteryx bilineata* (Sb; photograph: Manuel Sánchez-Mendoza), *Dermanura watsoni* (Dw; photograph: Gloriana Chaverri), and *Thyroptera tricolor* (Tt; photograph: Sébastien Puechmaille).

echoacoustic calls for communication is that their high frequency provides a private channel of communication that eludes detection by many predators and masking by many of the common low-frequency sounds in natural systems (Arch & Narins, 2008).

Both social calls and echolocation are known to be used by bats for social communication, yet mounting evidence suggests that echolocation can be used more frequently as a cue, unintentionally providing information to eavesdroppers, while social calls appear to be used primarily as signals, and are produced actively to convey information to conspecifics (Gillam & Fenton, 2016; Bohn & Gillam, 2018). Bats may eavesdrop on echolocation calls broadcast by conspecifics that unintentionally provide useful cues, such as the location of foraging sites that eavesdroppers establish by detecting feeding buzzes of foraging conspecifics (Barclay, 1982; Fenton, 2003, 2013; Dechmann et al., 2009; Voigt-Heucke, Taborsky & Dechmann, 2010; Bohn & Gillam, 2018). Potential consequences of this information transfer may be positive, such as in cooperative hunting (Dechmann et al., 2009), or negative, such as increased competition for food (Cvikel et al., 2015).

As with echolocation, using social calls for communication may entail both costs and benefits for bats. One cost of social call emission is the metabolic demands it places on individuals (Gillooly & Ophir, 2010), but the energetic basis of social call production has not been addressed in bats to date. Many studies show that several types of acoustic signals, particularly those emitted during courtship, allow predators to detect prey efficiently (Lindström et al., 2006; Möller, Nielsen & Garamszegi, 2006; Alem et al., 2011). Thus, the use of acoustic signals that are audible to predators, such as the low-frequency social calls emitted by many species, may also pose a risk to bats; again, this hypothesis needs to be addressed further, as no studies have yet been conducted. A potential benefit of using social calls for communication is that these signals can be transmitted over longer distances than echolocation pulses, given their lower frequency (Fenton, 2003, 2013; Bohn & Gillam, 2018). Also, the complex spectral characteristics of many social calls...
allow these signals to encode a large number of unique individual signatures (Wilkinson, 2003; Arnold & Wilkinson, 2011; Carter et al., 2012; Chaverri, Gillam & Kunz, 2013), which makes them ideally suited for individual recognition in large colonies (Wilkinson, 2003).

(3) Visual communication

Bat eyes are more effective for long-range detection, as their ability to resolve fine spatial details may be limited (Eklof et al., 2014). The functions of vision so far established or suggested are mostly limited to sensory ecology, including obstacle avoidance, food location, navigation and escape (e.g. Eklof, 2003; Boonman et al., 2013) whereas its involvement in intraspecific communication is almost anecdotal (Caro, 2013). The nocturnal habits of bats and the tendency of most species to roost in dark sites inevitably makes vision a secondary sensory modality to convey and receive messages (Voigt, 2014). Indirect clues that bats use vision to communicate are scant. Besides chromatic disorders, which are not rare (Lucat & Lope-Baucells, 2016), most bats are drab, with brown, grey, reddish or blackish fur, probably as an adaptation to camouflage while roosting (Caro, 2013). The nocturnal habits of bats and the tendency of most species to roost in dark sites inevitably makes vision a secondary sensory modality to convey and receive messages (Voigt, 2014). Indirect clues that bats use vision to communicate are scant. Besides chromatic disorders, which are not rare (Lucat & Lope-Baucells, 2016), most bats are drab, with brown, grey, reddish or blackish fur, probably as an adaptation to camouflage while roosting (Caro, 2013). Some species show colour patterns that may also have a communication function, such as the yellow carotenoid pigment observed in the ears, nose-leaf, and forearms of Ectophylla alba (Galván et al., 2016), or the conspicuous white facial stripes of other stenodermatine bats (Fig. 2).

Visually striking behavioural patterns may be common in aggressive contexts, e.g. Carollia perspicillata wing-shakes and extends its tongue in such situations (Fleming, 1988), or in courtship, when males may exhibit advertisement flights, wing shaking or hovering to attract females' attention (Vaughan & Vaughan, 1986; McWilliam, 1989). Visual displays are also common among epauletted fruit bats (Epomophorus wahlbergi) during courtship, when retractile tufts of white hair are erected by wing-flapping males (Adams & Snod, 2013). Although one of their likely roles is to convey visual messages, such movements may also help spread pheromones or, as in pipistrelle song flights (Barlow & Jones, 1997), to broadcast social calls over defended territories. Vision may also act in synergy with tactile communication, namely grooming. In Demeus youngi and Diphylla ecaudata grooming is elicited visually by a mirror reflection (Goodwin & Greenhall, 1961) and bats may imitate self-grooming conspecifics (Vaughan & Vaughan, 1986), overall suggesting a role for vision in grooming behaviour.

(4) Tactile communication

Tactile and vibrational communication are close-proximity ways to convey information: they require direct physical contact and so switching off mechanisms of ‘private spacing’ between individuals (Weber, 1973). This suggests that tactile communication will be mostly involved in cooperative or affiliative behaviours, as they may occur only when there is low aggressiveness between interacting individuals (Weber, 1973). Whether and what animals communicate by mutual contact is often difficult to understand and observe, as many forms of tactile displays are likely to occur primarily inside the roost where non-invasive observations are difficult (Kunz & Parsons, 2009); thus, despite probably being common, tactile communication is likely to be often overlooked (Hill, 1998).

In mammals, the main structures involved in tactile communication are body pressure receptors as well as the
fur and some specialized hairs such as vibrissae (Hill, 1998), particularly abundant on the muzzle and, in some cases, the feet (e.g. in molossid bats). The most common form of mammalian tactile communication is social grooming, a set of caring or comfort behaviours including licking, rubbing and scratching directed to another individual, sometimes in a reciprocal way (Dunbar, 1991; Alcock, 1998). Contacting another individual may convey information about the signaller’s identity or status, as well as preceding the onset of more complex cooperative behaviour. Nose-rubbing in wild Myotis bechsteinii often occurs before reciprocal grooming (Kerth et al., 2003). Likewise, reciprocal grooming is common among vampire bats (Desmodus rotundus) before they share food (Carter & Wilkinson, 2013), and they are known to perform reciprocal-grooming behaviour more often than other social species (Carter & Leffer, 2015).

Contact may also be used to memorise the identity of colony mates by refreshing an individual olfactory ‘template’, reinforcing social bonding and facilitating future cooperative behaviours. In T. brasiliensis, nose-rubbing is performed together with a specific vocalization, in individuals that were experimentally re-united after being apart, thus representing a ‘greeting’ behaviour probably aimed to reinforce social bonds (Bohn et al., 2008). Likewise, huddling (accomplished through physical body contact between bats whose bodies typically also vibrate) and reciprocal grooming in captive Pipistrellus kuhlii and Hylonycteris savii are more common among colony mates (Ancillotto, Serangeli & Russo, 2012; Ancillotto et al., 2014).

III. WHY DO BATS COMMUNICATE?

(1) Communication of identity

Although the study of communication in animals has largely focused on signals informing conspecifics or heterospecifics about external events, perhaps the most widespread form of communication is the transmission of signaller’s characteristics, such as species, sex, individual identity, social status or body condition (Fernald, 2014). Investigations on bats have mainly focussed on two communication channels that these mammals exploit to convey individual information, i.e. odour and sound, both of clear importance for nocturnal mammals that can rely little on vision. Here we provide a few examples of olfactory and acoustic signals used for conveying information about identity.

(a) Species discrimination

Little work has been done on odour-based discrimination of conspecifics versus heterospecifics. Two sympatric, morphologically similar species in the genus Saccolonyx (S. bilineata and S. lepura) carry species-specific scents in their wing sacs, and female S. bilineata prefer the wing sac odour of conspecific males to that of males from the sister species, in this way probably maintaining pre-mating isolation (Caspers et al., 2009). Results are less clear for the cryptic pipistrelles Pipistrellus pipistrellus and P. pygmaeus. Males of the former have a preference for odours (facial gland secretion and to a lesser extent urine) of conspecific females compared to those of the other species and vice versa. However, females seem not to prefer conspecific odours, which might help explain cases of hybridization suggested by studies of population genetics (Sztencel-Jablonska & Bogdanowicz, 2012). It is also possible, however, that females rely on other senses besides olfaction to recognize male conspecifics (Bartoniczka et al., 2010).

Investigations on the transmission of personal information among bats have more often focused on sound, both social and echolocation calls. Because social calls have, broadly speaking, a rather stereotyped species-specific structure, they clearly offer great potential for distinguishing conspecifics from heterospecifics (Fenton, 2003; Pfläzer & Kusch, 2003); yet most studies to date on the use of sounds for recognition have focused on echolocation signals. Overall, there are relatively few proven cases of communication of individual attributes by the presence of acoustic signatures in bats broadcasting frequency-modulated (FM) calls (Kazial, Kenny & Burnett, 2008; Yovel et al., 2009); the most interesting examples come from species emitting constant-frequency (CF) calls. Rhinolophids broadcasting CF calls may recognize echolocation calls of conspecifics from those of heterospecifics, and may also distinguish among pulses of other sympathetic species broadcasting similar calls (Schuchmann & Siemers, 2010). Acoustic divergence in sympatric species calling similarly has been explained as a way to avoid frequency overlap between species and maintain species-specific ‘private communication channels’ (Russo et al., 2007); in fact the problem posed by partial resting frequency (RF) overlap for species recognition may be overcome, possibly because other call features play a role in this process (Schuchmann & Siemers, 2010).

(b) Recognition and localization of group or colony members

Bats are known to discriminate among the odours of roost and non-roost mates, and this signalling modality may be particularly important during the process of recognition (Bloss, 1999). In choice experiments, pipistrelle bats (Pipistrellus pipistrellus) can quickly learn to discriminate among the odours of individuals from two different colonies, and results suggest that while scents are individual-specific, they may have a strong group signature. This latter finding may explain why bats learned more quickly to discriminate between colonies than they learned to discriminate among individuals (De Fanis & Jones, 1995). Colony-specific odour signatures may also be prevalent in a diversity of other species (De Fanis & Jones, 1995; Bouchard, 2001; Bloss et al., 2002), including big brown bats (Eptesicus fuscus; Bloss et al., 2002), Bechstein’s bats (Myotis bechsteinii; Säf & Kerth, 2005), fishing bats (Noctilio leporinus; Brooke & Decker, 1996), and Brazilian free-tailed bats (Tadarida brasiliensis; Englert & Greene, 2009), with concomitant effects on recognition (Bloss et al., 2002; Englert & Greene, 2009). In other species, such as the Angola free-tailed bat (Mops condylurus), it has
been shown that the number of individuals that can be recognized based on olfactory cues is inversely related to the size of the colony, suggesting that recognition is based on individual, and not group, signatures (Bouchard, 2001). This is an interesting finding, as it indicates that individuals have an extraordinary capacity to discriminate among many types of odours, because colonies are often composed of several hundred individuals (Happold & Happold, 1989). Although odour profiles of colonies match mitochondrial haplotypes of colony members, there is no link between individual odour and genetic relatedness, so that although scent may be used to recognize individuals and colony membership, it cannot provide information on kinship (Safi & Kerth, 2003).

Acoustic cues and signals are also important for recognition of group members. Contact calls represent a particular type of social call directed primarily towards roost mates; to facilitate recognition, social calls encode individual or group ‘signatures’. For example, in pallid bats (Antrozous pallidus), vampire bats, and Spix’s disc-winged bats (Thyroptera tricolor), social calls have individual signatures (Fenton et al., 2004; Arnold & Wilkinson, 2011; Carter et al., 2012; Gillam & Chaverri, 2012) which allow bats to discriminate, and preferentially join, group members within roosts but also during flight (Chaverri et al., 2013; Montero & Gillam, 2015). Contact calls may be additionally used to retrieve group mates before foraging (Boughman & Wilkinson, 1998). Interestingly, recent studies show that encoding signatures for recognition among an increasing number of group members may strongly explain social call structure (Luo et al., 2017a). Individual and/or group signatures in echolocation signals have also been recorded in some species, including the big brown bat (Masters, Raver & Kazial, 1995), the African large-eared free-tailed bat Otomops martiensseni (Fenton et al., 2004), the greater mouse-eared bat Myotis myotis (Yovel et al., 2009), and the greater sac-winged bat, S. bilineata (Knörrnschmidt et al., 2012). These differences in call structure among individuals and groups may allow bats to discriminate echolocation signals of different individuals based on familiarity (Kazial et al., 2008; Voigt-Heucke et al., 2010), which may further facilitate group activities such as foraging (Dechmann et al., 2009).

(c) Recognition of potential sexual partners and mate attraction

Bats are known to rely on both olfaction and sound for sex discrimination. For example, in Mops condylurus as well as in male Chaerephon pumilus, the sexes are distinguished by scent produced from the interaural and muzzle glandular areas. There are other cases in which sexually dimorphic glands may facilitate discrimination between males and females, yet in most cases there is no experimental evidence supporting this (Bouchard, 2001).

Regarding sound, evidence suggests there is call divergence allowing for sex discrimination. For example, RF is known to be sexually dimorphic in some species, usually with females calling at higher frequencies than males (Suga et al., 1987; Siemers et al., 2005; Yoshino et al., 2006; Chen, Jones & Rossiter, 2009) while the opposite pattern is rarely observed (Guillén, Juste & Ibañez, 2000). Again, if strictly based on RF values only, effective communication of sex would in theory require minimal frequency overlap between the sexes. This is only known to occur in Rhinolophus rouxi (Neuweiler et al., 1987), whereas partial overlap is common and absence of dimorphism is also documented (Russo, Jones & Mucedda, 2001; Russo et al., 2007), thus if echolocation pulses are used to distinguish between the sexes they must include other sex-specific features.

Apart from dimorphism in acoustic and olfactory signals, which may facilitate sex recognition in bats, there are also examples of communication displays associated with courtship and thus probably under sexual selection. Some species are known to use chemicals to attract sexual partners (e.g. Saccopteryx spp.: Gaspers et al., 2009), and scent glands may be coupled with tufts of fur, as with the conspicuous crests of male Chaerephon chupini (Fenton & Eger, 2002), to increase odour persistence. Females may select their partner by assessing his genetic quality from cues associated with personal odour; alternatively, an individual’s genetic quality might be expressed by the males’ capability to cope successfully with the energetic cost of scent signalling in male displays (Voigt & Von Helversen, 1999). Females may also signal reproductive condition to male roost-mates with a combination of odours and grooming (Rathnakumar et al., 2017).

Most known sexual displays involve acoustic signals; yet documenting these may not be trivial as they are rarely broadcast in captivity and can be difficult to record in the wild. Males may emit social calls to advertise their presence or attract females (Lundberg & Gerell, 1986; Barak & Yom-Tov, 1991; Barlow & Jones, 1997; Gebhard, 1997; Schmidt-French & Lollar, 1998). The structure of these calls varies from single signals to batches of calls organized into ‘songs’ (Smotherman et al., 2016). Songs are widespread in mammals, birds, frogs and insects (Scarry & Andersson, 1986; Gerhardt & Huber, 2002), and their complexity is thought to convey more information to females and potential competitors than simple single-element vocalizations (Freeberg, Dunbar & Ord, 2012). This also holds true for bats, whose advertisement songs, emitted either in flight or from roosts (Jaeklová, Horacek & Bartonicka, 2008), are often complex [e.g. Pipistrellus nathusi (Jaeklová & Horacek, 2011); H. saci (Nardone, Ancillotto & Russo, 2017)] and arranged in motifs featuring trills, chirps and buzzes (see Bohn et al., 2008; Smotherman et al., 2016). The elements composing mating songs appear to be stereotyped and possibly genetically inherited, and variation across individuals is achieved by combining different components within the song (Bohn et al., 2009a). Individual bats may also modulate, and thus adapt, song structure according to the specific social context (Bohn, Smarsh & Smotherman, 2013).

In addition to song, bats may use echolocation calls for sex discrimination, mate selection, or to detect and deter potential competitors. For example, male greater sac-winged bats use echolocation pulses to discriminate the sex of approaching conspecifics, responding to females with courtship songs and to males with aggressive vocalizations,
which might facilitate the defence of roost territories (Knörrnschild et al., 2012). Recent work on *Rhinolophus mehelyi* (Puechmaille et al., 2014) has provided evidence that RF values may be subject to sexual selection. In this species, echolocation peak frequency correlates positively with body condition in both sexes (but see Russo et al., 2001), providing an honest signal of individual quality. This case is especially interesting since there are few examples (reviewed in Jones & Siemers, 2011) of a clear association between body size or condition and echolocation call frequency. Moreover, in tests done in captivity, females prefer high-frequency males during the mating season and such males sire more offspring, in agreement with the hypothesis that call frequency values are under sexual selection (Puechmaille et al., 2014).

Other species use a combination of signal modalities during courtship. For example, male *Saccopteryx bilineata* broadcast mating calls and exhibit courtship displays from exposed tree trunks (Voigt & Von Helversen, 1999). Displays include olfactory, visual and acoustic signals (Bradbury & Vehrencamp, 1977; Davidson & Wilkinson, 2002; Voigt et al., 2008). Wing flapping (i.e. visual signals) facilitates the spread of chemicals to attract females and is combined with the emission of a complex ultrasonic song. Females select their partner by assessing his quality from song complexity, so that males singing more complex songs sire more offspring (Behr et al., 2004; Davidson & Wilkinson, 2004). Singing complex songs while flying is energetically expensive so it can be used as an honest signal of individual condition (Behr et al., 2006). An additional example of multimodal displays comes from male epauletted fruit bats (*Eptomops* spp., *Epomophorus* spp. and *Hypsipetes monstrosus*), which emit ‘honks’ comprising simple, monotone, audible emissions (Wickler & Seibt, 1976; Adams & Snode, 2013). Sound is intensified using unique and sexually dimorphic cheek pouches, so it can cover long distances to attract females to leks (Adams & Snode, 2013). Acoustic signals are coupled with visual displays such as intense wing flapping or exposing retractile tufts of white fur on the shoulders (Wickler & Seibt, 1976; Bradbury, 1977; Adams & Snode, 2013).

(d) Locating and recognizing dependent young

Communication between mother and offspring is crucial in species showing parental care (Beecher, 1991), as mothers often need to perform tasks such as recognizing and retrieving their own young. Effective mother–infant communication facilitates pup caring in crowded roosts while avoiding non-intentional allosuckling, and also helps protect young from aggression from strangers (Bohn, Moss & Wilkinson, 2009b). These tasks may be particularly demanding in species that form reproductive aggregations, called nurseries, i.e. groups of reproductive females that give birth in the same roost, where pups are left alone at night while females forage (Altringham, 2011). Mothers returning to roosts after foraging face the complex task of retrieving their own pup amidst the many others present in the colony. In large *Tadarida brasiliensis* colonies, females reunite successfully with their pup in >83% of nursing events (McCracken, 1984).

Besides using spatial memory (McCracken, 1993), females employ odour cues (Gustin & McCracken, 1987; Loughry & McCracken, 1991; De Fanis & Jones, 1995), at least over short distances, but also make use of acoustic communication, which is more directional and covers longer distances (Searcy & Nowicki, 2005).

Most infant bats produce contact, or isolation calls [i-calls] when separated from their mothers; such calls elicit parental care in females (Gould, 1975). Pups start calling only a few minutes after birth and use i-calls at least until weaning (Knörrnschild, von Helversen & Mayer, 2007; Carter et al., 2012). Such calls are multi-harmonic, their frequencies are lower than those of echolocation calls, and they are broadcast in stereotyped sequences (Gould, 1971) until the pup reunites with its mother (Schmidt-French, Gillam & Fenton, 2006).

Isolation calls have been found to attract mothers both in natural (Watkins & Shump, 1961; Bohn, Wilkinson & Moss, 2007) and experimental settings (Matsumura, 1979; Balcombe, 1990; De Fanis & Jones, 1995; Schmidt-French et al., 2006; Bohn et al., 2007; Knörrnschild, Feifel & Kalko, 2013). Call rates increase when pups are separated for longer periods (Matsumura, 1979; Mayberry & Faure, 2014) or their body temperature decreases (Camaclang, Hollis & Barclay, 2006), probably encoding the pup’s status or motivation and thus altering the mother’s response (Camaclang et al., 2006). Distressed *Eptesicus fuscus* young change i-call parameters to make calls similar to those produced at an earlier age and elicit a more rapid response from their mothers (Mayberry & Faure, 2014).

While females certainly respond to pup calls, it is unclear whether pups discriminate among adult calls. Although recognition is mutual in some species (De Fanis & Jones, 1995; Esser & Schubert, 1998), in others is unidirectional (Balcombe, 1990; De Fanis & Jones, 1996). Mother–infant reciprocal signalling and recognition is known for some species [*Rousettus aegyptiacus* (Kulzer, 1958); *Pteropus poliocephalus* (Nelson, 1965); *Myotis lucifugus* (Turner, Shaughnessy & Gould, 1972); *Rhinolophus ferrumequinum* (Matsumura, 1979)], and antiphonal calling – a duet between mother and offspring – may also occur (Matsumura, 1981; Brown, Brown & Grinnell, 1983; Balcombe & McCracken, 1992). In species showing unidirectional recognition, female echolocation or directive calls [emitted in response to i-calls (Brown, 1976; Matsumura, 1979; Esser & Schmidt, 1989; Balcombe & McCracken, 1992; Knörrnschild & von Helversen, 2008)] may encode individual identity (Yovel et al., 2009; Voigt-Heucke et al., 2010; Jones & Siemers, 2011) that is recognized by adults (Boughman & Wilkinson, 1998; Pfälzer & Kusch, 2003) but not by pups, which neglect their mother’s acoustic signals or olfactory cues (Balcombe, 1990; Knörrnschild & von Helversen, 2008; Mayberry & Faure, 2014).

Personal odour may also be used by mother bats to mark their own pups and recognize them subsequently. For example, *T. brasiliensis* use the scent of their own muzzle glands to mark their pups unambiguously (Gustin & McCracken, 1987). Finally, odours have been suggested...
to be used by juveniles to advertise their age in order to decrease aggression from adults at roosts (Nielsen et al., 2006; Ancillotto & Russo, 2014).

(2) Resources

(a) Foraging

Species feeding on patchy or only temporarily available food may actively defend trophic resources to increase their chances of survival and successful reproduction. Therefore, they often exhibit behaviours such as direct aggression or indirect (visual, olfactory and acoustic) displays to preclude access of competitors to their primary food sources (Brown, 1964). ‘Possession’ of a feeding patch, whether temporary or permanent (= territory) may be expressed by an individual through the signalling of its presence to avoid direct conflict with competing conspecifics or heterospecifics: this limits energy expenditure as well as the risk of physical damage associated with direct confrontation, and facilitates spacing among individuals (Carpenter & McMillen, 1976).

Bats that rely on ephemeral food resources, such as fruiting trees and insect swarms, or that more generally exploit sites where food availability tends to decline quickly, may defend their feeding territories or repel other individuals. For these tasks, bats use visual displays and, more often, species-specific calls, commonly comprising multiple harmonics and components (Pfalzer & Kusch, 2003), whose structural complexity and variation might represent a way to encode different information or motivation (Russo et al., 2009; Luo et al., 2017b). Using playback experiments, Barlow & Jones (1997) showed that Pipistrellus pipistrellus and P. pygmaeus social calls serve an agonistic function and are species specific as they repel only conspecifics from foraging sites. Another typical feature of these calls is that they mostly comprise low (sometimes audible to the unaided ear) frequencies, to increase their operational range (Pye, 1980).

There is evidence that the rate at which social calls are emitted is negatively related to food abundance, i.e. when resources are scarce bats emit agonistic calls more often. For example, male Cardioderma cor perform territorial songs from different perches around the area they share with a female, but only during the dry season, when food is scarcer (McWilliam, 1987). The same increase in call rate was detected over different nights in Lasiusus cinereus (Belwood & Fullard, 1984) and P. pipistrellus (Barlow & Jones, 1997), with more calls being emitted when insects are less abundant, and particularly when two or more bats forage at the same site. Agonistic social calls at feeding sites have been recorded from individuals chasing others to exclude them from the defended area, such as in L. cinereus (Belwood & Fullard, 1984) and Euderma mastacatum (Leonard & Fenton, 1983; Storz, 1995). Although agonistic social calls are often species specific, as competition is most likely to occur between conspecifics sharing the same ecological niche, in P. kuhlii and P. maderensis their structure is very similar because the latter originated from the former (Russo et al., 2009). In that case, crossed playback experiments have demonstrated that calls elicit interspecific reactions (Russo et al., 2009). Food defence is not restricted to insectivorous bats: foraging common vampire bats emit social calls during aggressive interactions (Sailler & Schmidt, 1978). Similarly, the frugivorous bat Pteropus giganteus vocalizes while also flapping its wings and showing its teeth, in response to the presence of both conspecifics and Cynopterus sphinx when feeding at fruiting trees (Nathan et al., 2009).

Bats may also communicate about food location, an important potential benefit of sociality in species that exploit ephemeral or unpredictable food sources, such as insect swarms or fruiting forest patches (Safi & Kerth, 2007; Kerth, 2008). Such calls may attract group mates or deter potential competitors, e.g. by including group signatures in the call structure. Greater spear-nosed bats (Phyllostomus hastatus) emit ‘screech calls’ in flight to coordinate foraging activities among group members and defend feeding sites (Wilkinson & Boughman, 1998). Group members recognize each other from their unique group signatures and discriminate non-group members (Boughman, 1997; Boughman & Wilkinson, 1998).

Several studies show that naïve bats learn a new foraging task, find a profitable feeding area, or learn to associate a specific cue with food, if they interact, either during flight or at the roost, with a knowledgeable conspecific (Wilkinson, 1992; Ratcliffe & Ter Hofsteede, 2005; Page & Ryan, 2006; Clarin et al., 2014; Rose et al., 2016). However, we still do not know how information about food location or palatability is transferred among individuals, and whether signals or cues are used for this purpose. While intentional information transfer is considered a cooperative behaviour in bats, we still need to gather additional data demonstrating that individuals actively transfer information to group members. Further studies should seek to uncover the signals used to communicate food availability, in addition to understanding the benefits and costs accrued by signalers and receivers during this process.

(b) Roosts

Roosts are important resources for bats, not only as suitable space for resting, but also as a refuge from predators and adverse environmental conditions (Kunz, 1982; Altringham, 2011). Bats also engage in important social activities at their roosting sites, such as lactation, copulation, social grooming, and learning (Wilkinson, 1986; Lausen & Barclay, 2002; Chaverri & Kunz, 2006; Geipel et al., 2013). Many types of structures are used as roosting sites by bats. Caves, for example, are used by a large proportion of bat species worldwide (Sagot & Chaverri, 2015), and are the most permanent roosting structure known (Levis, 1995; Altringham, 2011), often used by bat colonies for many years. Roosting structures also include buildings, hollow trees or tree cavities, termite nests, the flowers of carnivorous pitcher plants, and modified leaves, among many others (Kalko, Ueberschaer & Dechmann, 2006; Altringham, 2011; Grafe et al., 2011). Compared with caves, these other structures are typically more abundant, yet some are highly ephemeral.
Communication in bats

Wilson, 1974; Chaverri

small, cohesive social groups that roost inside the developing
to roost sites is Spix’s disc-winged bat. This species forms
of acoustic communication for recruiting group members
acoustic communication to recruit conspecifics actively to
communication. Studies show that many bat species use
locating a new one entails social coordination, and therefore
new sites. Because many bat species are gregarious, and
old roost structures deteriorate, individuals must locate
Plecotus auritus
inclusion Natterer’s (Myotis nattereri, Bechstein’s, and brown
tubular leaf (Chaverri et al., 2010). These leaves maintain
their tubular shape for relatively short periods of time, often
less than 24 h, and so bats must locate a new roost almost
every day (Vonhof & Fenton, 2004). Experiments show that
roosting bats emit two acoustic signals that allow them to
locate a new tubular leaf rapidly when they are disturbed
during the day. The first signal, termed an enquiry call, is
emitted by flying bats, while the second signal, or response
call, is emitted by bats that have located a roost but only
after hearing an enquiry call by flying conspecifics. Roosting
bats cease vocalizations as soon as other individuals enter
the tubular leaf (Chaverri et al., 2010). Both signals have
signatures that allow bats to discriminate, and preferentially
join, members of their own group (Gillam & Chaverri, 2012;
Chaverri et al., 2013). This call-and-response system has only
been recorded during the day and in this single context
(Montero & Gillam, 2015), suggesting that the main function
of this exchange of acoustic signals is the active recruitment
of roost companions.

While the use of social calls has also been observed in
many other species, there is no conclusive evidence that the
sole, or main, function of these acoustic signals is to recruit
group members to roost sites. Tent-making bats, for example,
can constantly emit calls in or around roosts at dawn, which is
the period when individuals arrive at their day-time roost (Gillam
et al., 2013). In the noctule bat, Nyctalus noctula, bats are also
known to vocalize often at the tree cavities that they use as
roost sites, and playback experiments demonstrate that these
calls elicit inspection and arrival by flying conspecifics, which
presumably may allow individuals to locate roosts and group
members quickly (Furmankiewicz et al., 2011). Broadcasting
social calls near roost sites also causes inspection of potential
roost sites in several other species of tree-cavity-roosting bats,
including Natterer’s (Myotis nattereri), Bechstein’s, and brown
long-eared bats (Plecotus auritus; Schöner, Schönér & Kerth,
2010). Pallid bats (Antrozous pallidus) also emit social calls with
individual signatures as they approach roosts, which attracts
familiar conspecifics (Vaughan & O’Shea, 1976; Arnold &

To recruit conspecifics to roost sites, bats may use other
sensory modalities, yet this has not yet been explored in great
depth. For example, tree-roosting Leisler’s bats (Nyctalus
leisleri) are known to perform ‘dawn swarming’, a highly
stereotyped set of behaviours performed before entering
roosts that includes fly-bys in front of the roost entrance,
landings, and leaps. This swarming apparently has a rallying
purpose, announcing the location of the roost site using visual
signals to other individuals in the vicinity (Nado & Kałnuch,
2013). Also, while olfactory communication is widely used by
bats (Dechmann & Safi, 2005), the few studies conducted to
date do not show that the smell of conspecifics improve the
location of roost sites compared to other sensory modalities
(Ruczyński, Kalko & Siemers, 2007). One study, however,
indicates that male pipistrelle bats use scent marks at or near
their roosts, which, coupled with acoustic signals, may help
females locate a roost site (Lundberg & Gerell, 1986).

(3) Antipredatory behaviour

Antipredatory communication is widespread among animals:
many species of birds, reptiles, amphibians and mammals
produce distress calls when they contact a predator. Different
roles have been proposed for distress calls (Klump &
Shalter, 1984), all aimed at deterring predation: alert kin
or non-related individuals, puzzle the predator or attract
conspecifics to elicit mobbing or heterospecifics such as
predators of the predator threatening the caller.

Bats in a stressful or dangerous situation emit distress calls
(Fenton et al., 1976), e.g. when caught by or near a predator,
handled by a researcher or confined to a narrow space (e.g.
Russ et al., 2004). Distress calls elicit responses in conspecifics,
but the message conveyed is not unequivocal. It is a common
experience of bat researchers that keeping bats in cloth
bags near mistnets increase capture success as trapped
individuals attract other bats, so distress calls commonly have
an attractive power at least over conspecifics. The attraction
exerted by distress calls on other bats was demonstrated in
several studies (August, 1985; Russ et al., 2004; Knörrnschild
& Tschapka, 2012; Carter et al., 2015). Distress-call structures
seem to converge across species, and are either broadband
and multi-harmonic or show a steep frequency modulation;
in both cases their frequencies are lower than in echolocation
calls (August, 1985; Russ, Racey & Jones, 1998; Russ et al.,
2004; Carter et al., 2015; Hechavarría et al., 2016) to increase
communication range.

When caught, Myotis macrodactylus juveniles broadcast
distress calls more often than adults, suggesting that they
might represent a request for assistance in a stressful
situation (Huang et al., 2015). In other cases, distress calls
act as alarm signals: when experimentally broadcast near
Chaerephon pumilus roosts, emergence behaviour is inhibited,
so roosting bats are warned of danger and avoid it by delaying
emergence (McWilliam, 1989). Moreover, in most cases
distress calls cross species boundaries and prove effective on
a range of species (August, 1985; Russ et al., 2004). European
pipistrelle species even respond to distress calls of species
from Madagascar (Russ et al., 2004).

Mobbing predators (by flying in a group towards them) has
been rarely observed. In a few cases this has been recorded in
response to the emission of distress calls, e.g. in Phyllostomus
discolor, towards a snake that had captured a bat (Hopkins
et al., structure of distress calls across species (Russ et al., 2004). Other species were not observed to attack a loudspeaker broadcasting conspecific or heterospecific distress calls (Russ et al., 1998, 2004). Approaching the source of distress calls may expose bats to a greater risk (Lima & O’Keefe, 2013) so the adaptive role of this behavioural response is debatable; however, distress calls may be used by bats for startling predators, such as diurnal and nocturnal raptors (Mikula et al., 2016), and thus increase their chances of escape (Conover, 1994). Distress calls by bats accidentally trapped in confined spaces may attract others (Avery, Racey & Fenton, 1984; Russ et al., 1998, 2004), sometimes leading to mass trapping (Russo & Ancillotto, 2015).

The low degree or absence of individuality in the structure of distress calls (Pfalzer & Kusch, 2003) suggests that they do not convey information on the emitter, which would appear unimportant whatever their function. Actually, as in birds (Johnson et al., 2003), the effect of distress calls on heterospecifics is achieved by strong convergence in the signal structure of distress calls across species (Russ et al., 2004).

(4) Cooperative behaviours

Besides playing roles in social activities such as finding and defending important resources, and engaging in antipredatory behaviour, communication can also help bats initiate and modulate other forms of cooperative behaviour. One of the best-studied examples of cooperation is food sharing in the common vampire bat, where individuals regurgitate food to starving conspecifics (Wilkinson, 1984). Studies have shown that in addition to food sharing, vampire bats also participate in unusually high levels of social grooming (Wilkinson, 1986; Carter & Leffer, 2015; Fig. 3). Social grooming plays an important role in the establishment and maintenance of food-sharing relationships in common vampire bats not only because this behaviour may strengthen social bonds that promote cooperation (Carter & Wilkinson, 2013), but also because grooming may serve as a tactile signal that indicates the desire to receive, or the intention to donate, food (Carter & Leffer, 2015). In addition to touch, olfactory communication may be important during cooperative interactions in vampire bats, as bats often sniff individuals before and after social grooming and food sharing (G. G. Carter, personal communication). Contact calls also seem to be important in helping recipients find frequent donors (Carter & Wilkinson, 2016), and other acoustic signals may be used to indicate the need to receive food; fasted bats emit social calls that attract donors to their location to regurgitate food to the begging bat (G. G. Carter, personal communication).

Another form of cooperative behaviour where communication is essential is the retrieval of non-volant pups that have fallen from cave ceilings. This behaviour has been observed in the cave-roosting greater spear-nosed bat, a species that forms highly cohesive social groups comprised primarily of unrelated females (McCracken & Bradbury, 1981). When pups fall, they emit isolation calls that adult females recognize as either belonging to a group or a non-group member (Bohn et al., 2007). In the former case, females typically attend to and guard the pups until the mother arrives to retrieve it. Unguarded pups may be subject to aggression and even killed by non-group members (Bohn et al., 2009b), so the help of group members may be critical for the survival of fallen pups that when retrieved may provide thermoregulatory benefits to other pups in the cluster (Wilkinson et al., 2016).

IV. FUTURE DIRECTIONS

The study of social communication in bats has made significant advances during the last 15 years. However, it still lags behind our understanding of communication in other taxa. If we focus on the sensory modality that has been most intensively studied in bats (i.e. sound), and on one particular role of this sense (e.g. to facilitate contact among group members), there remains a large discrepancy in our understanding of this large group of mammals compared to other mammalian taxa and vertebrates in general. Primates, for example, a mammalian order represented by a third of the species diversity described in bats, have been the subject of approximately 60 publications over the last 20 years that cover a wide diversity of findings. These studies mostly involve contact calls, including descriptions of call parameters, call function, individual recognition, vocal learning, dialects, group coordination and collective decisions, how the environment affects signal transmission,
and the effect of human activities on the production and reception of these signals. In bats, however, there are only around 22 published studies on this topic, with a much narrower focus of research. With such a large number of species and ecological diversity, a greater focus on bats would allow us to test broader and more far-reaching hypotheses on the evolution of animal communication systems.

There are many interesting avenues for future research that may allow us to increase understanding of social communication in bats. First, many bat species possess a well-developed sense of smell (Dechmann & Safi, 2005), and many species have what appear to be subcutaneous glands in several regions of the body that produce pheromones, such as the neck, scrotum, and between the ears. As described herein, there have been interesting developments regarding the role of olfactory communication and glands in species such as *Saccopteryx bilineata* and pipistrelles, but many species remain very poorly studied. Many mammals also engage in scent marking, particularly around territory boundaries, to deter potential competitors (Gosling & Roberts, 2001). Given that many bat species engage in territorial behaviour, it seems logical to assume that many species would also use scent marking to delineate territorial boundaries. However, this behaviour has only been observed thus far in a couple of species. Secondly, with regard to acoustic communication, there are countless avenues for future research, particularly given the rapid advances in our overall knowledge of bat acoustics. For example, hormones such as oxytocin are known to modulate social behaviour (Caldwell, 2017), but only one study to date has addressed its effect on social interactions, specifically the tendency to engage in social communication (Carter & Wilkinson, 2015). We also have no understanding of the potential costs to bats of the emission of social calls, specifically regarding energetic demands and increased risk of predation. The Acoustic Adaptation Hypothesis has been widely applied to other vertebrates (Ey & Fischer, 2009), and has provided clues as to why some species vocalize when and where they do. Again, no studies to date have addressed this in bats. Other studies have looked at communication networks in a diversity of species (Snijders & Naguib, 2017), with the potential to investigate which individuals are critical for maintaining social cohesion and group efficiency. This would also be a potentially rewarding research area in bats. Finally, while many species of bats are nocturnal, and visual communication is thought to be of minimal importance to these species, there are many others that are diurnal; for these, visual communication may play an important role, yet almost no studies have been conducted to date. Other nocturnal species engage in social interactions during the day, including grooming and copulating. Some of these species also have conspicuous colour marks that may play important, but thus far unknown, roles in social communication.

Bats represent a fascinating taxon to further our understanding of social communication given that many species are highly gregarious (Kerth, 2008) and long-lived (Wilkinson, 2002), increasing the chances of repeated social interactions and thus the need to communicate effectively with conspecifics. Bats also have strong perceptual capabilities in multiple sensory modalities, use a large diversity of roosting and feeding resources, and have highly variable life histories, thus providing a rich background to test hypotheses that will greatly improve our understanding of animal communication. Most importantly, we need to increase our knowledge on bat communication in light of human-induced environmental problems such as light and sound pollution, climate change, and the depletion of critical feeding and roosting resources. Some of these problems are known or believed to cause a reduction in many species’ foraging efficiency (Luo et al., 2014; Luo, Siemers & Koselj, 2015), yet we have no idea how these issues may affect communication through, for example, masking of visual or acoustic signals. The depletion of important resources may also affect social communication (Chaverri & Kunz, 2011), yet how this affects different species and their fitness remains to be tested. The study of social communication in bats is growing fast, and we hope this review will help set the stage for further discoveries.

V. CONCLUSIONS

(1) Bats comprise the second most diverse mammalian order, and in general are gregarious and long-lived, which increases the likelihood of social interactions and the need to convey a large number of messages effectively. They also use a diversity of feeding and roosting resources which require some degree of social coordination to find and acquire. Therefore, bats provide a rich background to test hypotheses that will greatly improve our understanding of animal communication.

(2) The most commonly studied signalling mode for social communication in bats is sound. Bats use sound for recognition and localization of conspecifics and group members including dependent young, recognition of sexual partners and mate attraction, to signal territoriality and availability of resources such as roosts, and to deter predators, among others. Unlike other signal modalities, sounds can be used for short and long-distance communication and they can convey a large diversity of messages and be transmitted in a range of habitats and light conditions. Sounds also transmit messages immediately as an event occurs, and thus are ideal for pinpointing the location of specific individuals.

(3) The two main types of acoustic signals that bats use are echolocation and social calls. Some of the costs of using echolocation calls for communication include their high attenuation rates and simple structure, which limits the amount of information that they can encode, yet there is no cost to producing them during flight, and their high frequency provides a private communication channel. By contrast, social calls are more energetically demanding and may be detected by predators but may also be transmitted over longer distances than echolocation pulses, and their
complex spectral characteristics allow these signals to encode more information.

(4) Olfaction is also a relatively well-known signalling mode in bats. Odour has advantages over acoustic communication as signals may persist long after a sender has departed, and are thus useful for conveying persisting information. As such, odours may be used for scent marking, which may help deter competitors and/or signal the location of resources to group mates. Bats may also use olfactory signals for short-range communication, such as for courtship, mate selection, and for locating dependent young. In bats, specialized glands secrete many volatiles used for communication, and their products may be mixed with other body secretions to create a large diversity of odour combinations.

(5) Other signal modalities used by bats during social communication include tactile and visual, yet both have been poorly studied. The nocturnal habits of bats and the tendency of most species to roost in dark sites makes vision a secondary sensory modality to convey and receive messages, yet the use of conspicuous behavioural displays during aggressive contexts and courtship indicates that vision may be readily used in these situations. Tactile and vibrational communication are signalling modes that are only useful when animals are in direct physical contact, suggesting that tactile communication is mostly involved in cooperative or affiliative behaviours. In fact, most studies that describe tactile communication in bats have recorded physical contact shortly before social grooming or other cooperative behaviours, such as food sharing, occur.

(6) The study of social communication in bats has made significant advances during the last 15 years, yet it still lags behind our understanding of communication in other taxa. We propose several potentially rewarding topics for further studies, including a greater focus on neglected sensory modalities such as vision and touch. Regardless of the focus of future studies, it is important to increase our knowledge on bat communication in light of many human-induced environmental alterations that may hamper bat social interactions and even the acquisition of critical resources.

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**Note:** The text extracted from the image contains scientific references and information that are not clearly formatted and need to be pieced together to form a coherent sentence. The references are cited in the text, but the exact context and proper citation are not fully visible. The references are in different formats, and the natural text representation is constructed based on the visible content and contextual understanding.